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The Natural History of the Oilbird, *Steatornis caripensis*, in Trinidad, W.I. Part 1. General Behavior and Breeding Habits[1,2]

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(Plates I & II; Text-figures 1-6)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, West Indies. The Station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe. (Zoologica, 1952, Vol. 37, No. 13, pp. 157-184).].

Contents

Introduction

Humboldt's original account established the main features of the Oilbird's unique way of life (Humboldt, 1817; Humboldt & Bonpland, 1817). In 1799 he visited the now famous cave near Caripe in the mountains of northern Venezuela. He described how he found it filled with hundreds of screaming birds, of the size of a fowl but with the aspect of vultures. He reported that the birds left the cave only at night to feed on the fruits of forest trees, spending all day, and nesting, deep within the cave, where their ear-splitting shrieks and snarls made them seem, to the intruder, more like devils than birds. The scientific name which he chose, *Steatornis,* marked another memorable feature: that the young birds become exceedingly fat; he described how they were collected and boiled down by the local inhabitants to give oil for cooking and for lamps.

Humboldt's two original specimens were lost at sea and it was not until 1834 that the first specimens reached Europe (l'Herminier, 1834). As more specimens became available they attracted a great deal of attention from the bird anatomists of the day (especially Müller, 1842; Sclater, 1866; Garrod, 1873; Parker, 1889; see also Wetmore, 1918). These investigations showed that *Steatornis* is almost certainly closer to the caprimulgiform birds than to any other group, but that even to them the relationship is

[1] Contribution No. 1,008, Department of Tropical Research, New York Zoological Society.

[2] This study has been supported by National Science Foundation Grant G 4385.

very distant, while in certain characters they resemble the owls, perhaps due to convergence. Analysis of egg-white proteins corroborates the relationship to the Caprimulgiformes (Sibley, 1960).

For over 100 years far more was known in detail about the Oilbird's anatomy than about its ecology and behavior. Among a number of accounts of visits to Oilbird caves, most of which added little that was new, mention must be made of the more prolonged visit to the Caripe cave by Funck (1844), the first naturalist to visit it after Humboldt and Bonpland, and of the observations made by Stolzmann (1880) in Peru, which contain a number of points of great interest (quoted less fully in Taczanowski, 1884). Then Griffin investigated the Oilbird's method of orientation inside the caves. He showed that they are able to avoid obstacles when flying in pitch darkness, and that they do so by a method of acoustic orientation akin to that of bats, except that the note given out is easily audible, not supersonic as in bats (Griffin, 1954). More recently, Pietri (1957) has given an account of the Oilbird in Venezuela containing some interesting observations on the birds' behavior when feeding. A short preliminary account of the present study has already been published (Snow, 1958). Apart from these, little has been written about the Oilbird in life that is not anecdotal. The remoteness of most of the caves where they live, and the inaccessibility of the nesting ledges, have prevented sustained field study.

A small colony of Oilbirds inhabits a gorge near the head of the Arima Valley in Trinidad, about three miles from the New York Zoological Society's Tropical Field Station. This colony is the most easily accessible in Trinidad; furthermore, the nests are more easily reached than those in any other Trinidad colony, and probably more easily reached than in any colony throughout the bird's range. The gorge is situated on a private estate and is carefully protected. A further advantage is that a good deal of daylight enters the gorge, which is only partially roofed over, and around midday the nests are well enough illuminated for the birds' behavior to be easily observed. The present paper is based mainly on observations made at this colony over a period of 3½ years.

Methods

Much of the information gained has come from frequent routine visits to the colony, usually once or twice a week but sometimes daily for short periods. A total of some 250 visits have been made, and they are being continued. At each visit the contents of the nests are checked, a food sample is usually taken, and any necessary weighing, measuring or banding of young birds is carried out. The food samples have been collected in catching trays made of fine wire mesh, slung on the slopes below the nests, and from the nests themselves.

From 1958 onwards all the young reared in the cave have been banded. In addition four adults have been caught and banded. No attempt has been made, however, to band all the adults, since the handling of an adult bird causes great alarm among the whole colony and makes the birds shy for some time afterwards. The handling of young birds has no such effect.

In December, 1957, a platform was erected, spanning the gorge at the same height as the nests and about 15-25 feet away from them. A blind was set on the platform and from it observations were made on the birds' behavior by day and night. By day most of the birds, accustomed to my repeated visits, returned to their nests and behaved normally soon after I entered the hide, though some of them remained aware of my presence. Between 10.00 and 14.00 hrs. all details of their behavior can usually be seen, unless the weather is overcast; before and after this time the light is dim and less can usually be made out. By night much can be learned by listening from the blind, and by occasional quick inspections of the nests with a flashlight. This has been the usual method employed. In addition some observations were made at night by means of a battery-operated infra-red "Snooperscope," but technical difficulties have so far limited the success of this method.

Acknowledgments

I am grateful to several persons and institutions for help in this work, and especially to the following: my wife, for help with the field work, particularly in catching the adults and banding adults and young; Mrs. Frederick B. Bang, for details of the Oilbird's olfactory apparatus; Mr. J. Barlee, for help in understanding the Oilbird's flight adaptations; Dr. William Beebe, for notes on the colony in the Arima gorge in earlier years, and for continuous interest and encouragement in the course of the work; Dr. W. G. Downs, for copies of photographs taken in the cave; Mr. J. Dunston, for making routine visits to the colony at times when I was unable to do so; and Professor J. K. Loosli, for analysing samples of the Oilbird's food. Above all I am indebted to Mrs. H. Newcome Wright, the owner of Spring Hill estate where the colony is situated, for her help and hospitality during the whole of the work. It is through her efforts that this colony, which is very vulnerable to human disturbance, has been able to survive.

This investigation, part of a wider program of studies on the ecology of neotropical birds, has been substantially aided by a grant from the National Science Foundation.

General Appearance, Stance and Locomotion

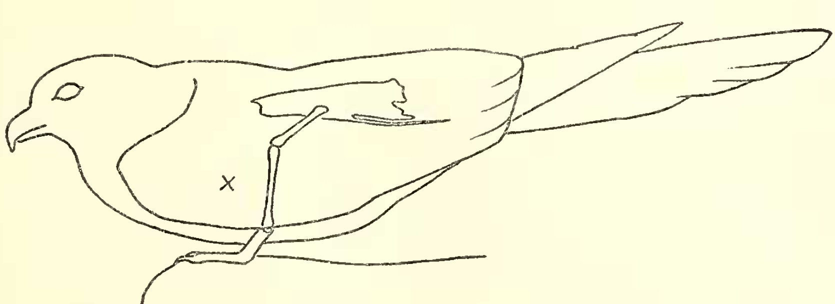
Several points about the Oilbird's general appearance deserve mention. It is a large bird, about 18 inches from beak to tip of tail and with a wing span of 3 to 3½ feet. The plumage is mainly rich brown with a scattering of white spots that are especially conspicuous on the wing coverts and outer secondaries. The body feathering is short and rather soft. The beak is strongly hooked and the upper mandible is notched on the cutting edge. The gape is very wide and the tongue short. Long vibrissae surround the beak and project mainly forward, beyond the tip of the beak. The legs are unfeathered and very short, but not weak; the claws are not strongly hooked. The tail is rather long, ample and markedly graduated. When it is folded the arrangement of the feathers is unusual: they form in transverse section an acute-angled inverted V.

Soon after observations were begun from the hide a slight but consistent color difference between the sexes was noticed. Males are a grayer, slightly darker brown, females paler and more rufous. Funck (1844) also noticed this difference, which has been of value in interpreting the behavior of pairs at the nest. (The sexed museum specimens that have been examined also show this difference, except that a proportion of the males tend towards the female coloring. These may be young birds, or in some cases perhaps "foxed" skins). Wing length is very variable in both sexes, but males average larger than females (nine Trinidad males, 307-333 mm., mean 320; eight females, 292-321, mean 307).

Oilbirds spend most of the daytime perched on the more or less flat surface of their nests. On such a surface they normally rest with the head held low, the body nearly horizontal but tilted somewhat forward, and the tail pointing slightly upwards. The feet are placed far forward, so that the bird appears to be crouching over them (Text-fig. 1; Plate I, Fig. 1). This "down-by-the-head" position is unusual for a bird; it is due to the fact that the Oilbird's legs are very short and come free from the body at a point rather farther forward than is usual in short-legged birds, while the center of gravity also lies well forward, the pectoral musculature being well developed, the sternum deep and the head large. Under such conditions a stable resting position on a flat surface can be achieved only by straightening out the leg joints as much as possible and rotating the whole limb as far forward as possible, and tilting the body head-downward, so that the breast is just above the feet. In this position the articulation of the femur with the pelvic girdle is well above the center of gravity. The bird thus rests with its weight, as it were, slung between the two more or less upright struts formed by its legs. This arrangement, which as a resting position is perhaps unique in birds, makes it mechanically impossible for the Oilbird to stand on one leg.

Ingram (1958), from an examination of specimens, concluded that the short, thick tarsus functions as an integral part of the foot, and that when the bird is perched both lie flat on the substratum. This is not so, however (Text-fig. 1; Plate I, Fig. 1). The tarsus is held within about 30° of the vertical, as in most other birds. Three of the toes point forward while the hallux projects inward approximately at right angles to the line of the body. Movement on the nest, or on any other flat surface, is effected by very short shuffling steps, a method well adapted to prevent the bird from suddenly stepping off the edge.

From the mobility of the hallux it has been



Text-fig. 1. Usual stance of Oilbird on nest, showing position of pelvic girdle and leg-bones, and approximate center of gravity (X).

suggested (Ingram, 1958) that when the Oilbird clings to narrow ledges all four toes point forward, as in the swifts (the pamprodactyl arrangement). In fact, in such a situation the toes are spread out more than when perched on a flat surface. The second and third toes point forward as usual, while the fourth (outer) toe may be held more to the outside of the foot than usual. The hallux still points inward or sometimes even backward (Plate I, Fig. 2). Bock & Miller (1959) have shown how a rather similar arrangement is most effective in enabling woodpeckers to cling to rough vertical surfaces, and for the Oilbird too it probably gives a surer grip on the rough ledges to which it clings than if all four toes pointed forward. For additional support, the tail is fanned a little and pressed hard against the rock face.

An Oilbird cannot, however, cling to a vertical surface, like a woodpecker on a tree trunk or a swift on a wall. Its claws are not very strongly hooked and its tail feathers are not stiffened. As Plate I, Fig. 2 and Plate II, Fig. 3, show, when an Oilbird clings to a small ledge or rough slope the feet are held far back, not forward, as in the woodpeckers, swifts and other birds adapted for clinging. An Oilbird can only cling in such a place if it can bring its center of gravity inside, *i.e.*, to the cliff side, of its feet; otherwise it would simply fall off. To do this, it must not only hold its feet well back but must also keep its head and breast well into the cliff side, an inefficient method which shows that Oilbirds are not primarily adapted for clinging to rock faces.

As mentioned above, Oilbirds are unable to support themselves on one foot. This is clearly seen when they scratch their heads. As in many non-passerine families, the foot is brought to the head directly from below, not from behind the wing. When the bird scratches, it lowers the wing on the same side as the foot which is raised, so that the carpal joint takes the bird's weight. Occasionally both wings are so lowered.

It has been supposed, from the conformation of the tarsus and foot, that Oilbirds are unable to perch in trees (Ingram, 1958). However, Stolzmann (1880) reported that they do so occasionally, and Pietri (1957) gives a detailed account of Oilbirds perching on the bare branches of trees at night. They are also able to alight on quite slender perches. When the birds were suddenly disturbed in a semi-open cave with a top entrance, a few miles east of the Arima gorge, a bird perched for a few moments on a slender woody vine that hung across the cave mouth. Since Oilbirds may be absent from their caves for six hours or more at night (p. 41), it is likely that they make frequent use of their ability to perch on trees. The scene in the well-known illustration in Brehm's *Tierleben* of Oilbirds perched on trees outside a cave apparently by day, though fanciful, is not physically impossible.

Aerodynamically the Oilbird is highly specialized for its way of life. Life in caves demands that it should be able to fly very slowly, hover, and turn and twist with agility, all within narrow confines. Its method of feeding, on bulky fruits often collected far from caves, again demands the ability to hover, and also to carry considerable weight. I am indebted to J. Barlee for showing how well these demands have been met, and for making the calculations given in Table I.

The Oilbird's wing combines, to a striking degree, low wing-loading with an extremely low aspect-ratio. (Text-fig. 2). Low wing-loading (weight/wing-area) enables a bird to fly slowly, manoeuvre easily and carry large loads. The very low aspect-ratio (wing-span/mean width) enables the Oilbird to achieve the necessary low wing-loading without having a large wing-span. This must be of special importance in negotiating the narrow passages of caves. The Oilbird's wing-loading is comparable to that of a harrier (*Circus* sp.) or an owl, both slow-flying birds which carry considerable weights (Table I), while its aspect-ratio is, Mr. Barlee informs me, one of the lowest known for birds of large size.

There are further refinements in addition to this major adaptation of wing shape. The wing has plenty of wing-tip slotting, to reduce stalling speed, and is deeply cambered, to give high lift at low speed. The ample tail further improves manoeuverability and gives extra supporting area when the bird is flying slowly and hovering (Plate II, Fig. 4). Barlee suggests that these adaptations may give the Oilbird a flight speed as low as one or two knots, which is in agreement with observation.

Stolzmann (1880) explained the inverted-V arrangement of the tail feathers as an adaptation to hovering. He described how, when hovering, the Oilbird rhythmically elevates and depresses the tail, as some hummingbirds do when feeding. He suggested that, owing to the inverted-V arrangement, the downward movement of the tail generates lift, while the upward movement meets with little resistance from the air. I have never seen a bird hovering for long enough, in good light, to be able to see the tail movement which Stolzmann describes. He appears to have been an acute observer and his suggestion deserves consideration.

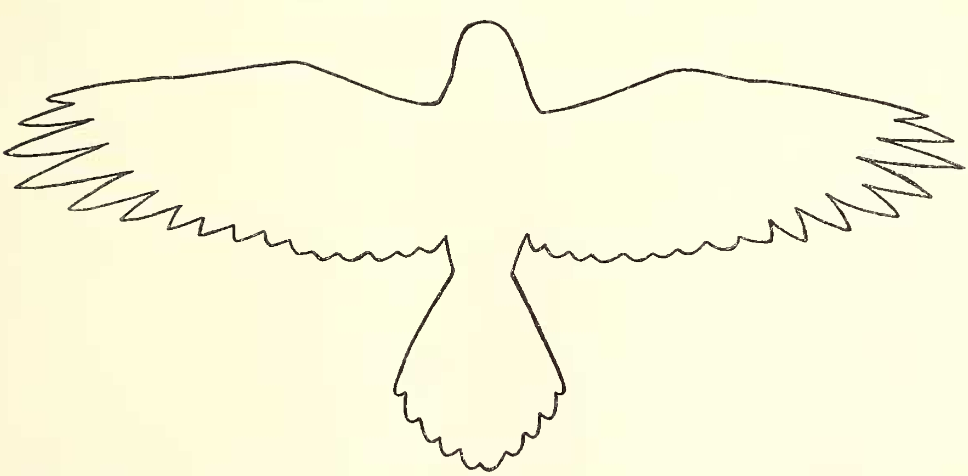
TABLE I. AERODYNAMIC CHARACTERS OF OILBIRD WING COMPARED WITH MARSH HARRIER AND LONG-EARED OWL

	Weight (gm.)	Span (cm.)	Wing-area ($cm.^2$)	Aspect-ratio (span/ mean width)	Wing-loading (weight/ wing-area)	Pectoralis major/ supracora-coideus
Oilbird	415	96.5	1450	6.4	0.29	15
Marsh Harrier (*Circus aeruginosus*)	510	124	1820	8.5	0.28	22
Long-eared Owl (*Asio otus*)	291	95	1270	7.2	0.23	12

High-speed flash photographs show that in slow flight the wingbeat is deep and the upstroke of the wing is propulsive (Plate II, Fig 5), as it has been shown to be for pigeons in rising flight (Brown, 1951). In hovering, too, the upstroke (which, with the body in a half-upright position, becomes a backstroke) must generate lift as well as the downstroke. Hence it would be expected that the muscles that raise the wing would be highly developed. The supracoracoideus, which is usually considered to be the chief muscle raising the wing, is however quite small (weight 2 gm., compared with 30.5 gm. for pectoralis major). In this the Oilbird agrees with most other birds of low aspect-ratio. Probably most of the power for the upstroke comes from the deltoid muscles, which are well developed (weight 2.5 gm.) and have a broad attachment along half the length of the humerus, rather than from the supracoracoideus, which in addition to being smaller has a mechanically less efficient attachment to the humerus.

In the open, at night, the Oilbird's flight is rather different from its flight in caves. The wingbeat is rapid and shallow. Doubtless the wings are held in a more sweptback position, and flying speed is thus increased by the reduction in wing area. As in the caves, the flight is quite silent. Stolzmann, who clearly had excellent opportunities for observing them by night, saw them occasionally dive down like falcons, with wings half closed. Speed of normal flight in the open has not been determined by observation, but Barlee suggests that it may be about 16 miles per hour. Flight speed may be important ecologically, as it must have a bearing on the time taken to fly to the food trees, and hence on the number of times that the adults can feed the young in the course of the night.

The method of feeding is not easy to observe in detail. In the Arima Valley birds have been watched feeding on trees of two kinds, *Ocotea wackenheimii* and *Trattinickia rhoifolia*. Invariably they have been seen to fly up to the tree, hover, and swoop away a moment later.



TEXT-FIG. 2. Outline of Oilbird with wings and tail fully spread. (Traced from a freshly killed specimen).

Occasionally a quick forward thrust of the head could be seen, as the bird seized a fruit. Pietri's account of Oilbirds feeding on *Persea caerulea* is similar. However, Stolzmann saw Oilbirds cling momentarily, with beating wings, when taking fruit from a lauraceous tree (probably *Nectandra* sp.), and Ingram (1960) has reported that when feeding at a palm (called Sabal, but probably *Livingstona*) they cling to the bunches of fruit for several seconds. In *Ocotea* and *Trattinickia* the fruits do not grow in large compact bunches, as in the palms. It is likely that Oilbirds adapt their methods of feeding to the type of tree, clinging when this enables them to pluck a number of fruit from a single bunch.

An analysis of the Oilbird's food will be given in Part 2 of this paper. Here it need only be said that the fruit taken varies greatly in size, from the small round fruits, about 4 mm. in diameter, of the palm *Geonoma vaga* to the relatively huge fruits, up to 60 mm. long and 30 mm. wide, of the lauraceous tree *Beilschmiedia tovarensis.* All the main fruits eaten are alike, however, in having a single relatively large seed surrounded by a firm pericarp. The pericarp is digested and the seed regurgitated. Regurgitation of the night's feed is completed by about 09.30 hrs. on the following morning.

Senses

Although orientation by sonar (Griffin, 1954) takes the place of visual orientation within the caves when the amount of light is reduced below a certain point, it is not known to what extent sonar would be effective outside the caves at night; in particular, it is not known how small an object can be detected by this method. This is a question that must be settled by experiment. Observation shows, however, that the Oilbird's eyes are very sensitive to light and whenever possible sight is used instead of sonar, and suggests that sonar is normally never used outside the caves.

Thus in the Arima gorge, when a bird is flying toward a dark recess the echo-locating clicks are uttered, but they slow down or stop as the bird wheels around toward a better-lighted part of the gorge. When the birds were watched in the evening leaving the Oropouche cave, several miles east of the Arima gorge, they clicked continuously as they flew down the narrow passage toward the cave mouth and stopped clicking as soon as they emerged into the open. I have never heard clicks from birds feeding at night. It may be noted that the Oilbird's eyes, though not very large, have a very wide pupil and a tapetum which shines bright red when illuminated with a light held beside the observer's eye.

In locating food it seems likely that the sense of smell is important, though here again experimental work is needed. For the following notes on the Oilbird's olfactory apparatus I am indebted to Mrs. Frederick B. Bang, who recently examined freshly preserved specimens from Trinidad as well as comparable material from other species of birds. The Oilbird has a relatively very large and heavily innervated olfactory organ, with one of the thickest mucous membranes of any bird examined. The nasal chamber is beautifully adapted to carry the incurrent airstream, after being initially filtered by the respiratory concha and anterior concha, straight onto this mucous membrane. It is of interest that the respiratory (middle) concha is relatively enormous, but the functional significance of this is uncertain.

Such a highly developed olfactory apparatus must surely have an important function. That it is used for locating food trees is suggested by the fact that many of the trees on which Oilbirds feed are spicy or aromatic, in particular members of the families Lauraceae and Burseraceae. It seems unlikely, however, that the sense of smell can be used for locating individual fruits; for this, sight is almost certainly used. Very many of the fruits taken are green when unripe and turn dark purple or black when ripe. That the birds nevertheless sometimes make mistakes is shown by the fact that the food samples collected in the caves often contain a small proportion of unripe fruits which have been regurgitated undigested. Pietri's account is particularly significant on this point. A party of Oilbirds watched feeding on *Persea caerulea* settled on trees when the moon was obscured by clouds, and began feeding again when the clouds had passed.

Within the caves the sense of smell could perhaps be used for locating the nest, which with the decaying fruit on it usually has an odor perceptible to the human nose, but it is unlikely that this is of importance in view of the undoubted accuracy of the birds' orientation by sonar. Once the bird is on the nest, the sense of touch probably plays the chief part in orientation with respect to the mate or young, and for this, as Ingram (1958) points out, the long, forwardly-projecting vibrissae are undoubtedly used. It may be noted that the birds themselves have a characteristic musty odor, which may perhaps play a part in individual recognition.

Whatever senses are used in the various activities related to food and to the nest, an extremely highly developed kinaesthetic sense may be postulated. It is therefore of interest that the Oilbird's cerebellum is unusually large (Bang, *in litt.*).

General Behavior and Daily Routine

At all times, whether breeding or not, adult Oilbirds spend most of the daytime in pairs, perched on their nests. Usually they perch side by side, facing outwards. For most of the time they are quiet; sometimes they sleep. Occasionally the silence is interrupted by an outburst of harsh calls, as perhaps when two birds on adjacent ledges engage in a tussle, with beaks interlocked, or an unestablished bird tries to land on a ledge near an occupied nest. Toward evening there is an increase in calling and general activity and birds begin to leave their nests and fly around. This period of restlessness lasts an hour or more before the departure from the cave begins.

In the Arima gorge the evening departure is difficult to study in detail as there are four ways of exit, up the gorge, down the gorge, and by two top holes. On September 25, 1957, watch was kept in the cave from 17.30 to 19.30 hours. From 18.00 to 18.45 there was great activity which gradually decreased as more and more birds left. At 19.00 the departure seemed to be complete. Inspection by flashlight, however, disturbed two birds which flew around for a few seconds and then left. The cave was then empty of adults except for one which was brooding a small nestling. In another watch, on December 24, 1957, most birds had left by 18.15. At 18.30 the flashlight revealed five adults still present, of which four were probably attending nestlings or eggs. On April 16, 1960, almost all had gone by 18.45, and by 19.00 the cave was empty of adults except for two which were attending nestlings.

By contrast with these observations of the departure of a small colony from a cave with several exits, the departure of a large colony from a cave with a single exit takes much longer. A watch was kept at the mouth of the Oropouche cave on the evening of October 25, 1958, a night of full moon. This is a large cave extending back about 400 yards into the hillside, with one rather small entrance hole. The first birds came out at 18.10. By 18.45, 102 had come out, and by 19.40, 62 more. In the next five minutes 11 more came out. Between 19.45 and 20.00 only one more bird came out and the departure seemed to be over. When the cave was entered at 20.05 the flashlight disturbed about 25 birds; almost certainly these were attending eggs or young. The birds had shown considerable hesitation in leaving the cave, repeatedly flying up to the cave mouth and turning back before finally coming out into the open. In addition, the narrowness of the exit passage had apparently forced the birds to "queue up" to leave and it was this, combined with their hesitation in leaving, that made the departure of the colony so slow. Most of the birds were in pairs as they emerged, with a small proportion single or in threes.

The birds seek food as soon as they leave the cave. Almost certainly they fly directly to fruiting trees that they already know. Thus the first birds arrived at a favorite food tree about half a mile from the Arima gorge at 18.20, 18.22 and 18.40 on three successive nights in December, 1958, suggesting that they had flown straight to it on leaving the cave.

I have not spent an all-night watch in the cave at a time when the birds were not breeding, in order to see whether they return periodically to the cave during the night. When they have eggs or young they return at intervals, as would be expected. In any case, the main return to the cave takes place shortly before dawn. On February 10, 1959, when no birds were nesting, one bird was already present when I entered the cave at 04.30. No other birds arrived until 05.35, when two or three returned. The number of birds present then gradually increased until 06.00, by which time all were probably present. On April 16, 1960, when most nests had young, the final return of the adults took place between 05.10 and 05.40.

Oilbirds are occasionally found in the daytime out in the open, sometimes far from a cave. Stolzmann (1880) mentions two such instances; he supposed that the birds had not left themselves enough time to return to their cave, and having been surprised by the oncome of daylight were waiting for nightfall before resuming their flight. But it seems very unlikely that an experienced bird would make such a mistake, and a more probable explanation is that these are mainly recently independent young birds, which have either failed to find enough food and have become weak or have become separated from their kind and lost.

Social Behavior

Since nesting activities occupy a large part of the year, and when they are not nesting Oilbirds still spend most of the daytime in pairs on their nests, there is little doubt that the pair bond must normally be permanent. The formation of pairs has not been observed. It is probable that the behavior connected with pair formation takes place at night, since it is at night that the birds are active and have the opportunity to meet birds from other colonies.

When the birds were watched leaving the Oropouche cave in the evening, twice a trio of birds, on emerging into the open, circled around each other, evenly spaced and with a swift, swooping flight. Similar behavior was seen on two occasions when birds were watched feeding in the Arima valley. After taking food, two or three birds circled around and around each other with low, clucking calls and a long, harsh "karrrr." It may well be that behavior of this kind is involved in pair formation. Stolzmann (1880) observed similar behavior in Peru and interpreted it as courtship.

In the daytime, one member of a pair sometimes preens its mate's head as they sit side by side on the nest. This behavior has only been seen just before the eggs are laid or during the laying period, except in one pair in 1959 which laid no eggs in that year (or lost them as soon as they were laid). The preening bird, with its eyes closed, works carefully over the other bird's head. The latter keeps its eyes open or only half-closes them. In nearly every case when this behavior has been seen, the preening bird has been known or presumed to be the male. The exception was a single instance when the presumed female, having been preened by its mate several times, was seen tentatively to preen its mate's head. This behavior is certainly a form of courtship and, from the times when it has been observed, must be closely associated with the period of copulation, but copulation itself has not been seen.

Relations between neighboring pairs are generally harmonious. When a bird alights on its nest, it sometimes provokes an outburst of excitement and calling from its neighbors, but such outbursts are short-lived. Occasionally, for no apparent reason, neighboring birds spar with their beaks and engage in tussles, gripping each other by the beak and twisting and pulling, with harsh calls, sometimes for several minutes on end. More prolonged fighting occurs when an apparently unestablished bird tries to secure a foothold on a ledge near an occupied nest. On May 10, 1959, two birds were watched trying repeatedly to secure a foothold in the same place, on a steep slope just below an occupied nest. Both were repelled. One of these, which was banded, was a young bird fledged in August of the previous year. These conflicts have been seen only shortly before, or during the early part of, the breeding season.

That there is some sort of cohesion between the adults of the colony when they are out at night, apart from the cohesion of the pairs, is apparent from observations on the times of feeding of the young which will be described later. Except for three nests in which the young were small and were fed more often, returns of the adults with food were concentrated into three main periods of about 20 minutes each, spaced about two hours apart. During these periods each nest, as far as could be ascertained by listening, was visited by one or two adults and the young were fed. This could only have been possible if the adults were keeping company with each other while collecting food.

The few observations that have been made on their feeding behavior also give evidence of a strong social tendency. When Oilbirds have been watched feeding at night in the Arima valley, up to five birds have arrived at the food tree within a minute, and after feeding for several minutes have departed within a short time of each other. Pietri (1957) also refers to their social behavior when feeding and describes how, when one bird of a feeding party was shot, the others called and swooped down low over the dying bird.

Except for the echo-locating clicks, the significance of the Oilbird's various calls has not been elucidated. When the birds are disturbed in a cave, the noise can be almost deafening; the calls range from clucks and rather low-pitched "hawking" sounds, reminiscent of the last of the bathwater going down the drain, to long-drawn-out, harsh screams. The calls made by aggressive birds on their nests, when another bird approaches, are similar. Birds flying in the open at night sometimes utter a shorter, less harsh "karr, karr" or "kuk, kuk," which is probably used in maintaining contact with other individuals. As Griffin (1958) points out, these is no sharp distinction between some of these shorter calls and the longer bursts of echo-locating clicks.

Whatever their signal function may be, the acoustic qualities of these calls are well suited to the conditions under which they are uttered. Many Oilbird caves are full of the noise of running water or breaking waves, so that, as for cliff-nesting sea-birds, very loud calls are essential. The harsh guttural quality of the calls, depending on a rapid succession of staccato sounds of many different frequencies, probably makes it easy for the other birds to detect the position of the calling bird (Marler, 1955). By uttering long-sustained calls, birds flying in the confined space of a cave can make their course known to the other birds. Thus social contact between the individuals can the more easily be maintained. The loud harsh calls are, however, not mere traffic signals. Purely for the avoidance of midair collisions, the echo-locating clicks are sufficient. Thus large numbers of Oilbirds can fly together in pitch darkness, uttering only clicks, but any disturbance will at once elicit a chorus of screams and snarls.

The Nest

As already mentioned, adults occupy their nests all the time, whether they are breeding or not. The nests in the Arima gorge are placed on narrow ledges, 8 to 15 feet above the stream bed. There are no suitable higher ledges. In other caves nests are normally much higher, partly because the caves themselves are much larger and partly because frequent raids on the caves have caused most of the lower and more accessible ledges to be abandoned.

The nest has a diameter of approximately 15 inches, with a shallow central depression and a slightly raised rim. It seems at first sight to be made of mud, and has been so described. It is, however, made primarily of regurgitated matter. When nest-building, the bird moves its head around the rim of the nest and with quick jerky movements plasters on semi-liquid matter which it allows to exude from the side of its beak. From the firmness of the resulting structure, it seems probable that saliva is important in binding together the regurgitated pulp, but this point needs investigation. The central part of the nest is formed from the accumulation of regurgitated seeds which the birds let fall; nest-building behavior does not, as far as I have seen, include work on any part except the rim. The faeces of the adults contribute little or not at all to the structure, for when defecating they turn and face inwards and shoot the faeces well clear, like other cliff-nesting birds. The young, too, turn when defecating but until they are well grown the faeces are usually deposited on the nest edge, where they contribute a little to the structure.

As nests are used year after year, they grow into low cylindrical mounds. Three of the nests in the Arima gorge have fallen away during the period of observation, as they became too large for the small ledges on which they were based. Two have been partly rebuilt. Parts of other nests have fallen away and been rebuilt. It is presumably by such a process of falling away and rebuilding that year after year the nests remain more or less the same size. The birds build up and repair the nest rim most actively in the few weeks before egg-laying begins, but the behavior also occurs when there are eggs and young.

The Eggs

The eggs are white ovals, slightly pointed at one end. The surface of the shell is slightly rough. The average weight of ten eggs, weighed soon after laying or early in incubation, was 20.2 gm. (range 17-22.5 gm.). Most eggs become spotted and blotched with brown soon after laying; this has led to erroneous statements that the Oilbird lays spotted eggs. The normal clutch is 2–4 eggs. (Clutch size will be dealt with more fully in Part 2 of this paper).

Although several daytime watches have been made at times when the birds were laying, there has been no record of an egg being laid during a period of observation. It seems probable that when about to lay, the female remains behind and lays her eggs before going off to feed.

The interval between the laying of successive eggs is unusually long and very variable. Daily visits to the colony over a period of up to two weeks may be necessary to ascertain the intervals between the laying of eggs in only one nest. As nests are not always well synchronized, daily visits over several weeks would be necessary in order to obtain exact information for the whole colony. This has not been possible, with the consequence that data on this point are fragmentary. The most accurately ascertained intervals between the laying of successive eggs were 2-4, 5, 6-7 and 6-7 days. In addition, minimum intervals of 6, 7 and 9 days were recorded. Between the laying of the first and third eggs in a clutch, the following intervals were recorded: 6-8, 7-9, 9, 9, 8-10 and 9-11 days. Other less exactly recorded intervals were consonant with these.

Incubation

The eggs are covered from the time they are laid. Complete clutches were never seen to be left uncovered (except after the birds had been frightened off the nest), but there were two observations of the eggs in incomplete clutches being left uncovered for 4 and 10 minutes while the parents perched on the edge of the nest. Both sexes incubate the eggs. The eggs lie very far forward under the incubating bird, between the chin and the legs, the whole rear half of the bird being slightly elevated. When the bird is relaxed the head is withdrawn between the shoulders and the eyes may be closed. The other bird, standing beside its mate, is usually alert, with its head held forward.

The lengths of the turns taken on the eggs are usually long, but very variable. Thus in a watch lasting three or four hours in the middle of the day, when the light is good enough to see details, only one or two completed spells may be observed. At nests where the sexes were known, females were recorded incubating for just over twice as long as males (1,129 as against 504 minutes), but this was due almost entirely to one nest, at which the female alone was seen to incubate. At the other nests the total time spent by the male and female on the eggs was nearly equal, and the few completed spells recorded for the two sexes were of similar length: males, 4, 32, 96 and 109 minutes; females, 7, 29 and 95 minutes. These spells are shorter than average, as the majority of the longer spells overlapped the beginning or end of the watch and so their complete length was not known.

The change-over is effected silently and without ceremony. Usually the incubating birds gets up off the eggs and shuffles to one side, while the other bird takes its place. Shuffling around by one or both birds may continue for several minutes before they settle down and become still again. Sometimes the non-incubating bird takes the initiative by becoming restless, shuffling about, and perhaps inserting its head beneath the incubating bird as though to ease it off the eggs. At the nest where only the female was seen to incubate, the male periodically became restless. Once after apparently trying to rouse the female from the eggs he performed nest-building movements, but without regurgitating any material, probably a displacement activity. Once he spent most of the watch on another ledge a few feet away from the nest.

Two experiments suggest that the Oilbird's egg-retrieving behavior is very poorly developed. One egg of a clutch of three was moved four inches from the other two, towards the edge of the nest. The male soon returned and incubated. Sitting on the two eggs, he looked at and occasionally touched the third egg with his beak but made no attempt to roll it back. After about a minute he sat quietly, ignoring the third egg. A few days later at the same nest one egg was moved three inches from the other two. The male again returned to incubate. When he had settled down the third egg was lying about one inch in front of him. He gradually shuffled it underneath him by moving forward himself a little and touching the egg with his beak so that it rolled a little. When the egg was nearly touching him he finally poked it underneath him. The whole process took three minutes.

Nests are usually surrounded by regurgitated seeds but these do not usually remain in the central depression of the nest with the eggs. This suggests that the incubating bird moves them, though this has not been seen. Sometimes, however, as many as three of the seeds of the palm *Jessenia oligocarpa* lie with the eggs. They are easily the largest of the seeds regularly taken by the birds in the Arima gorge and are apparently near enough in size to be accepted as eggs when they are regurgitated into the nest.

The eggs hatch at approximately the same intervals as the intervals between laying. For a day before the egg hatches the young bird can be heard cheeping inside. It emerges from the shell by cutting a circular cap from the broad end of the egg. The hatching process is quick; a young bird that was just starting to chip the shell at 15.30 hours was fully hatched at 17.00 hours. There were several instances of chipped eggs being hatched by the time of the next visit 24 hours later, and no cases of prolonged hatching.

The broken eggshells are not cleared away promptly by the parents; they often remain on the nest for a day or two before, like the regurgitated seeds, they are pushed, or perhaps picked up and dropped, over the edge. During a watch of nearly four hours an adult brooded the newly-hatched young with half an eggshell lying beside her; several times she fumbled with the broken shell but made no attempt to remove it.

The incubation period (measured from the time of laying to the time of hatching) is 32-35 days. Table II gives the most accurately determined periods for a number of marked eggs. In most cases there is a possible error of one day or a day and a half either way, as it was not usually possible to visit the colony frequently enough to give greater exactitude. It will be seen that there are no consistent differences in incubation period between eggs of different position in the clutch, which indicates that the eggs are not merely covered but effectively incubated from the time they are laid.

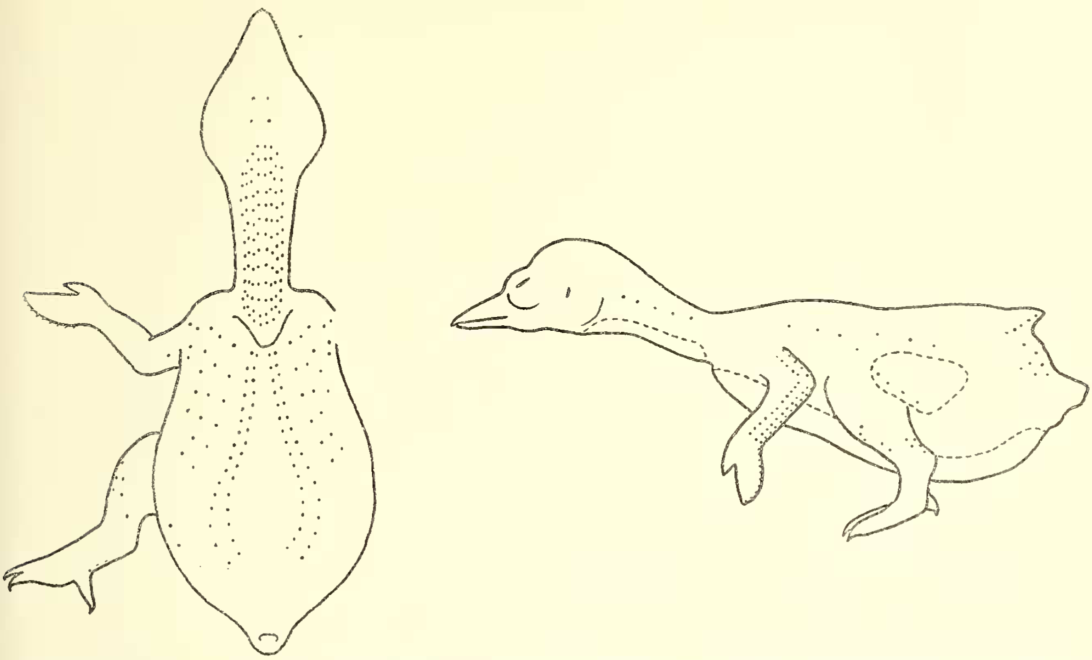
TABLE II. INCUBATION PERIODS

Egg 1	Egg 2	Egg 3	Egg 4
32 (±1)	32½ (±1½)	32 (±1)	34 (±1)
33½ (±½)	34½ (±1½)	33 (±1)	
33½ (±1½)	34½ (±1½)	33½ (±½)	
		34	
		34½ (±½)	
		35½ (±½)	

THE YOUNG

The most striking feature of the development of the young Oilbird is its extreme slowness. Young Oilbirds do not usually leave the nest until they are between 95 and 120 days old. During this time they lay down the great deposits of fat which have led to their being exploited for oil, attaining around the age of 70 days a weight much greater than that of the adult, and then losing weight for the last 30-50 days as their feathers develop.

Growth and Development.—The young bird at hatching weighs from 12 to 15.5 gm. It is naked except for some sparse down, chiefly on the under side. (Text-fig. 3). The amount of down at hatching varies; it is always thickest on the under surface, while on the back and flanks some



TEXT-FIG. 3. Distribution of down feathers on newly hatched Oilbird. Each dot represents one feather. Areas shown in detail in left-hand figure (ventral view) are outlined by broken line in right-hand figure. Area enclosed by broken line behind thigh in right-hand figure contains many feather rudiments visible below skin, but down sprouting only where shown. (Specimens vary individually).

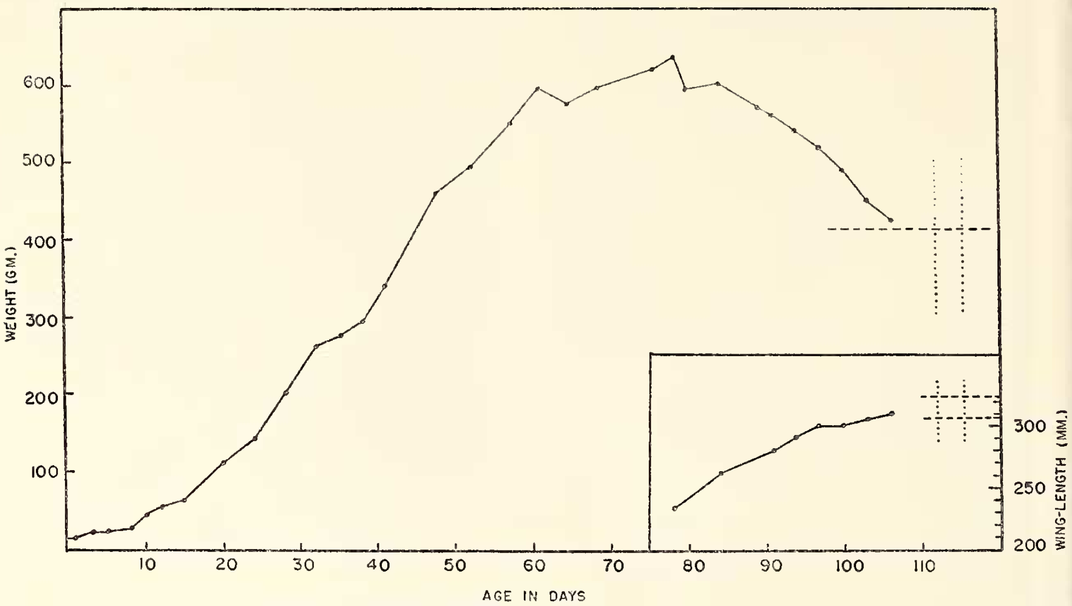
birds have a little down at hatching, or very soon after, while in others it does not burst through the skin until a few days after hatching. These first down feathers are short, pale gray and highly branched. In the second week after hatching a second generation of down feathers appears as black streaks beneath the skin. These second down feathers, which are darker gray and much longer, come from the same rudiments as the first and bear the first on their tips as they begin to break through the skin in the third week. Beneath some of the first down feathers on the ventral surface, especially towards the posterior end, no black streaks appear, and these down feathers are not succeeded by any others.

The first feathers of adult type, those of the tail, secondary coverts and scapulars, burst from their sheaths at the age of about 35 days. Thereafter the feathering of the wings and tail, head, back and underparts, in that order, grows steadily. By the age of about 70 days the nestling is quite like an adult, except that the wings and tail are very short and the body is still mainly downy below. It is noteworthy that there is not only no juvenile plumage but also no juvenile appearance of the head and beak. The nestling, when ready to leave the nest, is indistinguishable from the adult. Being adapted to complete darkness, the nestlings are without the visual signs which elicit parental behavior in other birds.

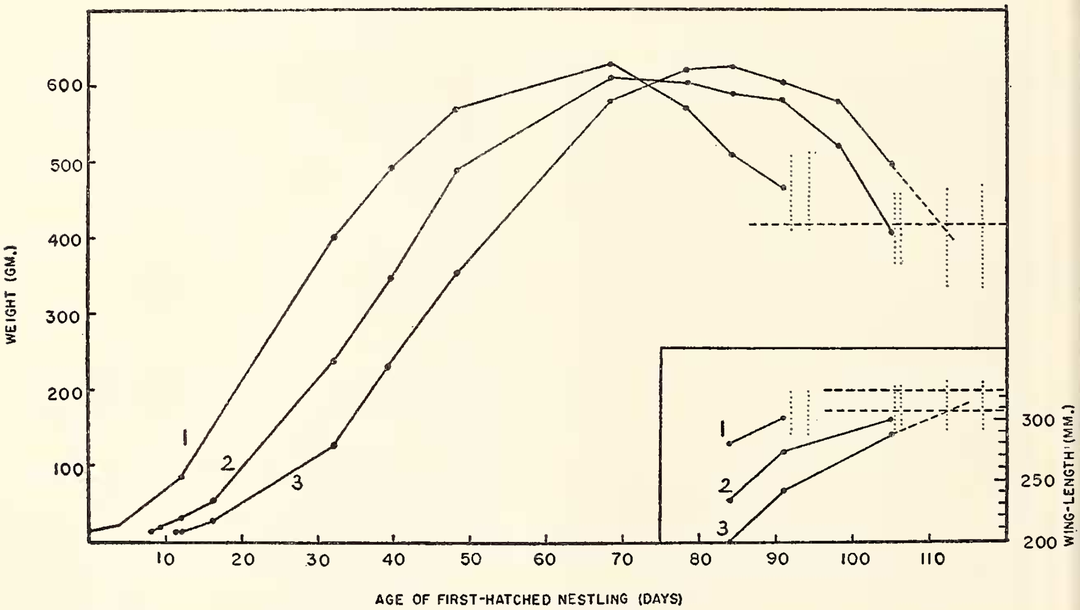
In Table III the main changes in the appearance of the nestling are tabulated. Because of the very long development, an accurate knowledge of these changes is necessary if the breeding season is to be dated from a single visit to a colony with eggs and young. It will be noted that there is great variability in the state of development of different birds of the same age.

Text-figs. 4 and 5 show the growth in weight of a single nestling and of a family of three, with the wing lengths in the last two or three weeks. It will be seen that the young birds leave the nest at the time when the decreasing weight and the increasing wing length have simultaneously reached the adult values.

The Nestling Period.—Whereas small young are sometimes restless during the day, and even beg occasionally (see next section), large young are inactive. Until very shortly before they leave the nest they usually show no tendency to fly when disturbed or even handled, at least during the daytime. (The one exception, a bird 109 days old, flew quite strongly when I rather awkwardly tried to turn it in the nest in order to read its band number). This is probably due in part to their being less active during the day, but also,



TEXT-FIG. 4. Growth in weight and wing length of a single nestling Oilbird. The broken horizontal line in the weight diagram shows the mean adult weight (415 gm.). The two broken horizontal lines in the wing length diagram show the limits of adult wing length. The vertical dotted lines indicate the period within which the nestling left the nest.



TEXT-FIG. 5. Growth in weight and wing length of a family of three nestling Oilbirds. Conventions as in Text-fig. 4.

and more importantly, to their being accustomed to frequent harmless disturbances. Thus when a boatman climbed up to some nests in a sea cave where the birds are still exploited by the local people, two nearly fledged birds left their nests and fluttered down into the sea. For the first few days after the young birds have left the nest they sometimes return to them by day, but

TABLE III. DEVELOPMENT OF NESTLING OILBIRD

Day	Description:[1] feather development	Weight (gm.)	Weight Limits	Wing (mm.)	Wing Limits
1	Nearly naked above, short sparse down below; eyes closed; squeaks when handled	12	12-15.5	—	—
5	As before, but larger	22	20-30	—	—
10	Wing feather rudiments visible as dark points (apparent on day 8)	40	30-75	—	—
15	Vibrissae sprouting; rudiments of second generation of down feathers as short black streaks on body; eye slits beginning to open; bird about 4½ inches long	65	50-120	—	—
24	Down feathers bursting out all over body; eyes open but not widely	145	100-230	—	—
30	Down prominent all over body; bird about 6½ inches long	230	120-300	—	—
35	Secondary coverts and tail feathers just beginning to sprout from sheaths	275	160-440	—	—
40	Tail feathers about 5 mm., secondary coverts 3-4 mm. beyond sheaths; primary coverts sprouting	330	240-500	—	—
50	Head feathers well out of sheaths (burst about day 47); scapulars, wing coverts and tail feathers forming almost complete covering of upper side; whole of body still downy	450	290-570	—	—
60	Body still downy; feathers growing on throat	580	390-610	—	—
70	Back well feathered; feathers growing on under side of body	595	560-650	190	—
80	Appearance like adult, but wing and tail short	595	550-650	240	160-260
90	Appearance like adult	565	520-600	280	200-300
100	Appearance like adult	490	420-550	300	240-305

[1] Description is based on a nestling whose rate of development was average. Weight limits and wing limits are limits for all nestlings which fledged successfully.

as soon as they are disturbed they fly off at once. Thus the fledging period can be measured quite exactly as the interval between hatching and the time when the young bird first voluntarily leaves the nest.

Only a few periods could be ascertained exactly. Usually they could be determined only within a few days, owing to the fact that it was rarely possible to determine both the hatching date and fledging date exactly. All fledging periods ascertained within limits of eight days or less are given in Table IV. There is a great difference between the shortest, 88 days, and the longest, 125 days, but most (71%) fall within 100 and 115 days. There is a tendency for the youngest member of a family to have a longer nestling period than its nestmates. This was certainly in some cases, and probably in all, because their early development was slowed down through competition for food with the older nestlings. Text-fig. 5 shows an example of a family in which this happened.

The full length of a single nesting, from the laying of the first egg to the fledging of the last young, is commonly round 150 days. The longest recorded, for a family of four all successfully reared, was 168 days.

Behavior of the Young.—For about the first 25 days after hatching, the young are brooded by the parents. They lie with their heads under the wing or breast of the parent bird; as they become larger the head often protrudes from between the parent's wing and body. They frequently thrust their heads upward toward the parent's neck, body or wing, apparently seeking contact; having gained it, they will stay motionless with the neck awkwardly kinked and the beak pointing upward. Occasionally they make food-begging movements, thrusting their head up at the parent's beak and nibbling at it. But, except perhaps when they are very small, the young are not usually fed by day (see next section).

The call of the young at hatching, and for a day or two before hatching, is a high-pitched cheeping. Later, by the age of 20 days, it develops into a loud, rather hoarse squeak, which becomes louder as the chick grows older. Large nestlings, when begging, utter a chorus of shrill but rather hoarse squeaks. By the time they are

TABLE IV. FLEDGING PERIODS

	Position in Family[1]			
	(1)	(2)	(3)	(4)
Family of 4	111 (±4)	112 (±2½)	110 (±3½)	125 (±2)
Families of 3	114 (±2)	111 (±3)	125	
	104 (±3½)	100 (±3½)	104 (±4)	
	98 (±3½)	98 (±2)	106 (±2)	
	109 (± 3)	109[2]	114 (±2)	
	93 (±2)	99 (±1)	103 (±2)	
	99 (±2)	104 (±3)	110 (±1½)	
	(Died at 62 days)	112 (±2½)	>116	
Families of 2	119 (±3½)	121 (±3½)		
	108 (±2)	115 (±3½)		
	101 (±2½)	102 (±2)		
	(Died at 42 days)	102 (±2)		
Families of 1	102 (±4)			
	112 (±2)			
	100 (±3½)			
	88 (±3)			

[1] In families in which one of the nestlings died in the first few days after hatching, this nestling has been left out of consideration in placing the other nestlings in their positions in the family.
[2] This bird flew on being disturbed (see text).

well feathered they begin to utter, if alarmed, the harsh screams of the adult.

They begin to preen themselves at the age of about 20 days. From the age of a few days, when defecating they turn, back towards the nest rim, and deposit the faeces on the edge of the nest. When they are larger the faeces are shot clear of the nest edge, as in the adult.

For about the first 50 days after hatching, the young rest with the lower surface of the body, the tarsus and the foot in contact with the substratum. Toward the end of this period they are able to raise the body clear of the substratum when shuffling about the nest. Later they begin to stand with the body clear of the nest, their weight supported only by the tarsus and the foot, and finally, by the age of about 75 days, they can stand on the foot only, with the tarsus held at an angle of 45-60°. Advanced young can clamber efficiently up quite steep slopes. To do this they not only grip and push with their feet but pull themselves up with the beak and dig in the leading edges of the wings. This behavior is of obvious value in enabling them to regain the nest if they are accidentally pushed out. They are very conservative in the position which they occupy in the nest. If taken out and replaced in different positions they shuffle and clamber over each other until they have regained the old positions.

Parental Behavior.—As already mentioned, for about the first 25 days the young are brooded by the parents. Usually only one bird at a time covers the young, but at one nest with four young both parents were seen to cover them for part of a watch. The number of young probably affects the length of time for which they can be brooded; at two nests single nestlings were brooded by day at the ages of 29 and 30 days, a longer time than was recorded for broods of two or more. At night one adult stays with the young while they are small; larger young are left by both parents. Thus during evening watches one adult remained on each of four nests with young 3-6, 12-18, 20 and 30-40 days old, while both parents departed from six nests with young 49 days old or more.

Many hours of watching have shown no evidence that the young are ever fed by day, except perhaps when they are very small. Very small young sometimes become restless, thrust their heads up jerkily toward the parent's head, and utter the food-begging call. Occasionally the parent has then been seen to lower its beak towards the nestling and itself make slight jerky movements. On such occasions some semi-liquid food may be passed to the young, but the adult's position, crouching over the young chick with lowered head, makes it almost impossible to see the details. From the 12th day, and perhaps earlier, the young are fed, at least partly, on whole undigested fruits.

Observations on the feeding of the young were made during an all-night watch on April 16-17, 1960. On this night four nests, all adjacent to one another, contained three young each, aged from 49 to 58 days, while three other nests contained, respectively, three young 12-18 days old, one young 20 days old and four young 30-40 days old (Nest K). When the evening departure of the adults was over, at about 19.30 hours, one parent remained at each of the three nests with smaller young, while both parents had gone from each of the four nests with large young. The first feeding was at Nest K, with four young 30-40 days old. It began at 20.51 and continued, with pauses, until 21.18. The first feed at the other two nests with small young was at about 21.00, but as these nests were more distant from the hide, and very close to each other, further detailed observations were not made on them. Although the darkness was total, it was easy to tell when a family was being fed. The adult on arriving would fly around for a little time, its position being shown by the echo-locating clicks. As it approached the nest to land the clicks would become more rapid and then suddenly cease as the bird landed. At once there would be a shrill chorus of squeaks from the chicks, which would continue at greater or lesser intensity while the feeding lasted. The other nests where no feeding was taking place would by contrast be almost or completely silent.

At 21.20, two minutes after the feeding was over at Nest K, inspection by flashlight showed that both parents were still present. At 22.00 only one was present. In the course of the night there were five more bouts of feeding at this nest, and perhaps a sixth: at 22.13-22.27, 23.33-23.44, (00.05-00.06, not certain, and in any case very brief), 01.29-01.37, 03.44-03.50 and 05.22-06.15.

At the four nests with large young, feeding began much later. There was one short feed at one nest only at 23.02-23.06, after which the parent departed again. Nothing further happened till 01.35 when a great burst of feeding activity began and lasted until 02.05. During this period there were at least seven landings by adults on the nests, followed by outbursts of begging calls. At 02.26 there was a single landing followed by a short feed. There was then over an hour without activity. The second main feeding period was from 03.42 to 04.06, when there were at least six, and probably eight, landings by adults followed by bursts of begging calls. There was a minor feed at 04.42-04.43, when only two adults landed, and a final main feeding period beginning at 05.35 and continuing until dawn. During this feeding period at least five adults landed. Thus there were three main feeding periods in the night, during which all or nearly all of the parents brought food, 01.35-02.05, 03.42-04.06 and 05.35-06.15, and three minor feeds by single birds or two birds, at 23.02, 02.26 and 04.42. The total number of recorded landings followed by feedings was 21 or 23. Probably one or two others were missed. Thus each of the eight adults attending the four nests brought food on average about three times during the night. Probably, with some exceptions to account for the three minor feeding periods, each bird brought food once during each of the main feeding periods.

The fact that the main feeding periods were synchronized at the four nests with large young (and also, though less well, at the three nests with smaller young) strongly suggests that the adults were foraging in company. Presumably they were feeding themselves during the six hours after they had left the cave and before the first main feeding period.

As it grew light, at 06.00, the last feeding was still in progress and it was possible to see the birds at the better-illuminated nests. At Nest K all four young were seen craning their heads up toward one of the parents, squealing shrilly. When being fed, the chicks half-turn their heads so that their beaks interlock with the adult's beak. The shrill begging calls cease abruptly at the moment the beaks interlock. Neither beak is opened very wide. As the adult regurgitates the food, its head and that of the nestling with it moves in short quick jerks. At the nests with large young the feeding was most vigorous; in the half-light these nests appeared to be filled with a heaving mass of birds. When the light improved it was possible to see that as adult and young both pushed strenuously during the feeding, with beaks interlocked, they reared up together with the head of the chick pointing obliquely upward and that of the adult downward. The adults were clearly under great physical strain. They could be seen pushing with their feet and would sometimes flap their wings to avoid falling backward. In this attitude both parent and chick would rear and heave together for a minute or more.

It could be seen that there was keen competition between the chicks of each family for the attention of the parent with food. At the only nest with four young, feeding continued longer than at the other nests, and the smallest chick of the four continued to beg for several minutes after the others, when the parents apparently had no more food left. Competition for food probably accounts for the slow early growth of the last-hatched nestling, mentioned earlier, and for the occasional death of small chicks, but there has been no evidence that nestlings have suffered from shortage of food in the later stages, when they need far more.

The Food of the Young.—During the first few days after hatching, semi-digested food is probably given to the young, as nestlings up to the age of ten days have occasionally regurgitated fruit pulp but not seeds. Also, as already mentioned, adults sometimes appear to pass semiliquid matter to very small young during the day. Later, whole fruits are fed to the young. The earliest age at which a nestling, when handled, has regurgitated a seed is 12 days. A nestling 15 days old, when taken from the nest after its last feed at dawn, regurgitated four seeds in the course of the day, almost certainly too small a number to represent the whole of its last feed. Thus the change from a pulp to a whole-fruit diet is probably gradual.

A full analysis of the Oilbird's food is reserved for Part 2 of this paper. Here only a few special points will be mentioned. Except that they are not given very large fruits, such as those of the palm *Jessenia oligocarpa*, the nestlings are fed on the same fruits as the adults themselves eat. The chief of these, during the periods when the food of the young has been studied, have been the palms *Euterpe oleracea* and *Bactris cuesa;* the Lauraceae *Ocotea oblonga, Phoebe elongata* and one unidentified; the burseraceous trees *Trattinickia rhoifolia* and *Dacryodes* sp.; and an unidentified, probably myrtaceous tree. Like the adults, the nestlings digest the pericarp and usually regurgitate the seeds. Very small seeds, however, may be either regurgitated or passed through the intestine. Most of the seeds of the night's feed are regurgitated by midmorning. Several times nestlings have been removed from the nest soon after their last feed, kept for the day and returned to the nest in late afternoon. Of the total of 428 seeds regurgitated by these nestlings, 306 (71%) were regurgitated before 09.00 hours, and all except 12 (97%) by midday.

On May 14/15, 1960, an attempt was made to estimate the amount of food given to a nestling in the course of the night. Two nests were cleared of all regurgitated seeds in the evening. Next morning three nestlings were taken from these nests at dawn, immediately after the last feed, and all the freshly regurgitated seeds lying by their beaks (hence almost certainly not regurgitated by the parents) were collected. The results, given in Table V, show that each nestling received approximately one-third or one-quarter of its body weight.

Stolzmann (1880) kept a nestling Oilbird for about three weeks. After feeding it at first on various kinds of unsuitable food he was able to obtain fruit of a *Nectandra* sp. (Lauraceae), one of the Oilbird's chief food trees in Peru. From his description the bird was then about 70 days old. Two experiments, made on different days, both showed that the bird was able to eat 14 fruits at a time, and that it regurgitated the first seed half an hour after it had eaten and the last seed one hour after it had eaten. This bird was almost certainly undernourished, which may explain the very short time taken for regurgitation compared with the nestlings studied here. At the same time his experiment shows that regurgitation can begin very soon after the food has been eaten, and suggests that under natural conditions at least a proportion of the seeds from the first feeds of the night will be regurgitated before dawn. This is confirmed by the present study. About one-third of the seeds regurgitated by the three nestlings in Table V had been regurgitated before they were taken from the nest. On the seven further occasions when nestlings have been taken from the nest at dawn (without earlier clearing of the nests and collecting of the fresh seeds regurgitated before dawn), the seeds regurgitated in the course of the day have never represented a feed of more than one-sixth of the nestlings' weight.

These young birds that have been removed from their nests have regurgitated a considerable number of whole, undigested fruits, the proportion varying between individuals and according to the kind of fruit. Fruits of the palm *Euterpe*, with a rather hard pericarp, have been regurgitated whole much more often than any other kind. Proportionally more fruits have been regurgitated whole early in the morning than later. Though the disturbance of being removed

Table V. Amount of Food Eaten by Nestling Oilbirds in the Course of a Night

Nestling	Age in Days	Weight of Nestling (gm.)	Number of Fruits Eaten	Total Weight of Fruit Eaten (gm.)[1]
Oldest of 3, Nest F..................	56	525	86	126
Oldest of 4, Nest K..................	40	350	73	103
Youngest of 4, Nest K...............	30	120	20	35

[1] Total weights of fruit calculated from the following mean weights of individual fruits: *Bactris cuesa,* 1.9 gm.; *Euterpe oleracea,* 1.3 gm.; *Ocotea oblonga,* 0.6 gm.; *Dacryodes* sp., 2.8 gm.

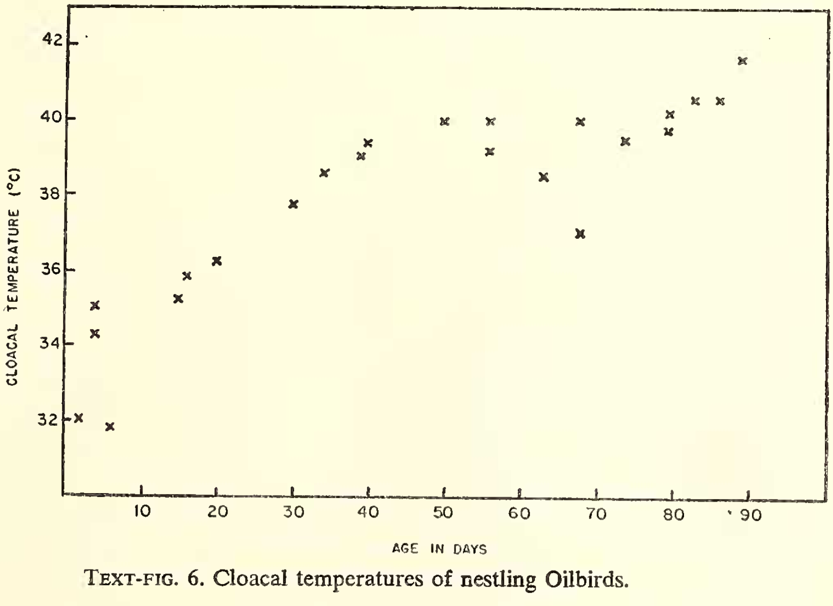
from the nest may cause some premature regurgitation, this is probably not the full reason for the regurgitating of whole fruits, since collections of food in catching trays below the nests regularly contain a proportion of whole fruits, especially during the seasons when the young are being fed.

Temperature Control and the Fat Deposits.—Small young feel cool to the touch after they have been left uncovered for a few minutes, and they rapidly become cooler. In order to study nestling temperatures, cloacal temperatures were taken with a quick-registering mercury thermometer as soon as possible after arrival at the colony (Text-fig. 6). Cloacal temperatures of 31.8° to 35.0° C. were recorded for nestlings up to six days old, while three nestlings 15, 16 and 20 days old had cloacal temperatures of 35.2°, 35.8° and 36.2° respectively. For older nestlings temperatures of 37.0° and over were recorded, most being between 39° and 41° from the age of 40 days onwards. (One very low reading for a nestling 68 days old may have been due to the thermometer lodging in a mass of faecal matter on the point of being expelled).

The ability to maintain body temperature appears to be acquired at the age of about three weeks. Thus the temperature of four young aged 2-6 days fell at the rate of between 1.3° and 2.3° in 10 minutes after being uncovered, while that of three young birds 15, 16 and 20 days old fell at rates of 1.0°, 0.6° and 0.3° respectively, and temperatures of older nestlings have usually not fallen appreciably during exposures of up to half an hour. Air temperatures at the nests are around 22° C. at midday, falling to about 18° at night.

In addition to the acquisition of temperature control, the age of about 25 days marks three other important and related changes in the life of the young Oilbird. The down feathers are bursting out all over the body (Table III). The young bird's weight is increasing rapidly (Text-fig. 4), probably due to a relative increase in fat deposits as well as to an increase in over-all dimensions. At the same time the parents are ceasing to brood the young bird by day, and at night they are beginning to leave it for several hours while they are out foraging.

There is little doubt that the thick down is important in enabling the nestling to maintain body heat, and it seems probable that this is also an important function of the deposits of fat. Deposits of fat in other young birds with slow development, especially Tubinares and swifts, have usually been considered to be reserves against periods of food shortage. These are birds in which the ability to find food is greatly dependent on the weather, and even when conditions are favorable the parents may have to travel long distances in obtaining it. For the Oilbird, however, there is no evidence that the nestlings are liable to undergo periods of fasting. The indications have been that food has been consistently abundant, and the ability of the adults to find the food does not seem to be much affected by weather. Throughout the breeding season in each year, as already mentioned, a proportion of the fruits brought to the nests have been regurgitated intact and dropped over the edge of the nests.



TEXT-FIG. 6. Cloacal temperatures of nestling Oilbirds.

Adaptations to Cliff-nesting

Cliff nest-sites are safe from most predators; indeed it is because of this that natural selection has favored their use in various groups of birds. If they are also in darkness, they are of course completely safe from visual predators. But suitable cliffs are not numerous, whether in caves or not. Hence cliff-nesting birds tend to defend their nests jealously once they have gained possession of them, but at the same time tolerate the close proximity of birds of their own kind and often of other species. Furthermore, in order to nest safely on a cliff a bird's behavior must be such that it does not knock the eggs or young off, and the young themselves must have behavioral adaptations preventing them from falling off. Cullen (1957) has shown how many of the morphological and behavioral characters of the Kittiwake (*Rissa tridactyla*), which distinguish it from other gulls, are attributable to its cliff-nesting habit. In the Oilbird, too, several adaptations to cliff-nesting are apparent, though in this case there are no close relatives with which it can be compared.

Nest sites suitable for Oilbirds are extremely limited in number, being restricted to a rather small number of caves in Trinidad and parts of northern South America. This has probably been the chief factor in the evolution of their highly social nesting behavior. It also probably accounts for the continuous occupation of the nest throughout the year, since a pair, once dispossessed, would find it very difficult to establish themselves again.

In the Kittiwake, cliff-nesting is associated with the relaxation of various anti-predator features. The same tendency is evident in the Oilbird; in particular, there is complete relaxation of all features that help to protect the nest against visual predators. Thus the adults are rather tame when on the nest, predators are not attacked, the eggs are white, and the chicks are not camouflaged.

If the nest site is safe, slow development of the eggs and young is not a serious disadvantage. Several authors have commented on the general correlation between safety of nest site and length of incubation and fledging period in birds, although no detailed study has yet been made. The Oilbird's development is exceptionally slow; among land birds only the California Condor (*Gymnogyps californianus*) is known to have a longer fledging period (Koford, 1953), while that of the Bateleur Eagle (*Terathopius ecaudatus*) is almost exactly the same (Brown, 1955). Such a slow development could hardly have been evolved if the nests were subject to such heavy predation as are those of most tropical birds (see, *e.g.*, Skutch, 1945); and in fact the evidence is that they are subject to little disturbance except from human beings. However, it is unlikely that the slow development can be attributed simply to the great safety of the nest site. It is probable that the Oilbird's specialized diet, of low protein content and containing a large indigestible fraction (the seeds), necessitates a slow development. If this is so, cliff-nesting and fruit-eating must have been intimately bound up with one another in the Oilbird's evolution.

Egg-rolling behavior is of little use to a cliff-nesting bird, whose eggs, if they are not in the concave nest-cup, are likely to be lost over the edge. It is not surprising therefore that the Oilbird is in marked contrast to the ground-nesting nighthawks, some of which are known to be able to move their eggs many feet, by pushing them or carrying them in the beak, and which do so repeatedly if disturbed. Likewise, when the young Oilbird has hatched, it is safe only if it remains in the nest-cup, and here again its tendency to stay still and maintain contact with its nest mates may be contrasted with the mobile behavior of young nighthawks. Remaining still in the middle of the nest is not due to inability to move, as even when they are quite small young Oilbirds move backward to the nest edge in order to defecate. Their ability to climb with feet, beak and wings gives them a chance to save themselves if they should nevertheless go over the edge of the nest. The parents' contribution to the safety of the young, as of the eggs, is limited to their tiny shuffling steps, which prevent them from kicking anything off the nest, or indeed from effectively moving any obstacle from their path.

Ecological Factors in the Evolution of the Oilbird

The Oilbird's combination, unique for a bird, of fruit-eating and nocturnal habits is undoubtedly due to its evolution from an originally nocturnal or crepuscular ancestor. As already mentioned, anatomical evidence suggests that the Oilbird's closest affinities are with the Caprimulgiformes, though it has certain characters in common with the owls. A consideration of feeding behavior, however, makes it almost certain that they are in fact closest to the Caprimulgiformes. All other caprimulgiform birds seize insects or other small animals in the mouth and swallow them whole, the feet not being used at all. Owls on the other hand seize their food in the talons and tear it up with the beak. Oilbirds, as we have seen, pluck fruits with the beak and swallow them whole. It is an easy transition to this method of feeding from the typical caprimulgiform method, but from the owl's method the transition is almost inconceivable.

We may then regard the Oilbird as the most extreme product of the rather limited adaptive radiation of the caprimulgiform stock. Since many of the larger diurnal birds of tropical forest are mainly or entirely frugivorous, it is perhaps not surprising that this food supply should have been exploited by one nocturnal bird. However, for an originally insectivorous caprimulgiform bird, the change to a fruit diet must have involved a number of ecological problems. The Oilbird's solution of these problems has had effects on every aspect of its life.

For the fruit-eater, forest trees in fruit are, essentially, temporary and discontinuous pockets of abundant food whose location is always changing. For a nocturnal fruit-eater, the short distance at which such pockets of food can be seen, or otherwise perceived, is an added problem. For a strong-flying bird there is no apparent advantage in searching for such food singly or in pairs, or in maintaining feeding territories, and in fact the parrots, toucans and other large fruit-eating forest birds are generally social feeders, as also are the fruit-eating bats. It is probable, therefore, that the change from an insect to a fruit diet in the ancestral Oilbird stock involved the enhancement of social and gregarious behavior at the expense of territorial behavior.

It is probable, too, that the Oilbird's large size, compared with that of most other caprimulgiform birds, was another consequence of the change to a fruit diet. It must have been a great advantage to be able to exploit the larger fruits, up to two inches or so long, of the tall forest trees, which form the main food of the large diurnal fruit-eating birds, since these not only give more nourishment for every fruit taken but are also much more conspicuous at night than the smaller fruits of second-story trees and shrubs which provide much of the food of the smaller frugivorous birds.

Increasingly social habits, increased size and a diet of fruit must have eventually necessitated radical changes in breeding behavior. In particular, increase in size and probably also the fruit diet (comparatively poor in proteins) must have lengthened the period of development of the young. At some point in its evolution the Oilbird must have faced in acute form the "choice" between either making the nest extremely inconspicuous, as do most other caprimulgiform birds and probably its own ancestors, or else making it extremely safe. Its large size, its fruit diet, which involves the accumulation of much regurgitated matter around or under the nest, its awkwardness in trees and lack of complex nest-building behavior (common to all the Caprimulgiformes), must all have favored the choice of a very safe nest site. Of the two main types of safe nest site available, cliffs and hollow trees, there is little doubt that natural selection would favor the former as being safer than tree holes and less sought after by other creatures. Cliff-nesting, as already mentioned, is usually associated with social breeding behavior; hence both for feeding and for nesting natural selection must have favored gregarious as against territorial tendencies. (It is perhaps instructive that one large fruit-eating cotingid, the Cock-of-the-rock, *Rupicola*, has adopted the same type of nest site, on cliffs or in shallow caves, and breeds semi-socially).

Presumably, then, the first step in the evolution of cave-nesting was from the ancestral site (probably the ground or on tree stumps) to cliff-ledges in the open, and it was at this stage that the rudiments of the echo-location faculty were evolved. Pressures of predation probably then led to the seeking of deeper and deeper recesses, until the perfection of echo-location allowed the birds to occupy the deepest caves, and so opened up for them a wealth of nest sites that were completely safe (until the arrival of man) and for which no other creatures competed.

Summary

An account is given of the general behavior and nesting of the Oilbird, based on 3½ years' observations.

Oilbirds are gregarious cave-dwelling birds, almost certainly of caprimulgiform stock. They spend all day in caves and fly out at night to feed on the fruits of forest trees.

The Oilbird's stance is peculiar, the body being tilted forward and the very short legs rotated as far forward as possible. Aerodynamically they are highly specialized for flight within restricted spaces and for load-carrying.

Sight is well developed and is used whenever possible. The sonar method of orientation, discovered by Griffin, is used only when there is not enough light. There is some evidence that the olfactory sense is important in food-finding.

Daily routine and social behavior are described. The birds leave the cave at dusk and return before dawn. They are gregarious while feeding. The pair bond is probably permanent. Aerial displays, probably connected with pair formation, have been seen at night. Courtship behavior on the nest consists of the preening of the female's head by the male.

The nest, eggs and young are described. The breeding cycle is very slow; eggs are laid at in-

tervals of several days, the incubation period is usually 33-34 days, and the fledging period 90-125 days. The young become very fat, reaching a weight half as much again as the adult's weight at about the 70th day. There are two sets of down feathers, followed by the growth of the adult plumage.

The young are fed at long intervals during the night, large young three or four times, smaller young five or six times a night. The food of the young is the same as the adult's. Nestlings eat about one-third or one-quarter of their body weight during each night.

The young acquire temperature control at the age of about three weeks. Both the thick down feathers and the fat deposits are considered to be important in maintaining body temperature.

The ecological aspects of the Oilbird's evolution are discussed. It is argued that the original change from an ancestral insect diet to a fruit diet led to increased gregariousness, increased size, slower development, the adoption of cliff nest-sites, and finally, with the perfection of echo-location, to the colonization of pitch-dark caves.

Literature Cited

Bock, W. J. & W. de W. Miller

1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. Amer. Mus. Novit., 1931, 45 pp.

Brown, L.

1955. Eagles. Michael Joseph, London.

Brown, R. H. J.

1951. Flapping flight. Ibis, 93: 333-359.

Cullen, E.

1957. Adaptations in the Kittiwake to cliff-nesting. Ibis, 99: 275-302.

Funck, N.

1844. Notice sur le *Steatornis caripensis* (Guacharo incolarum). Bull. Acad. Roy. Sci. Bruxelles, 11 (2): 371-377.

Garrod, A. H.

1873. On some points in the anatomy of *Steatornis*. Proc. Zool. Soc. London, 1873: 526-535.

Griffin, D. R.

1954. Acoustic orientation in the oil bird, *Steatornis*. Proc. Nat. Acad. Sci., 39: 884-893.

1958. Listening in the dark. Yale University Press, New Haven.

Humboldt, A. von

1817. Voyage aux régions équinoxiales du Nouveau Continent, fait en 1799, 1800, 1801, 1802, 1803 et 1804 par Al. de Humboldt et A. Bonpland. Vol. 3. Paris.

Humboldt, A. von & A. Bonpland

1817. Mémoire sur le Guacharo de la caverne de Caripe. Recueil d'observations de zoologie et d'anatomie comparée. Vol. 2. Paris.

Ingram, C.

1958. Notes on the habits and structure of the Guacharo *Steatornis caripensis*. Ibis, 100: 113-119.

1960. Guacharo feeding habits. Ibis, 102: 140.

Koford, C. B.

1953. The California Condor. National Audubon Society, New York.

L'Herminier, F.

1834. Mémoire sur le Guacharo (*Steatornis caripensis* (Humboldt)). Nouv. Ann. Mus. Hist. Nat. Paris, 3: 321-331.

Marler, P.

1955. Characteristics of some animal calls. Nature, 176: 6-7.

Müller, J.

1842. Anatomische Bemerkungen über den Quacharo, *Steatornis caripensis* v. Humb. Arch. f. Anat., 1842: 1-11.

Parker, W. K.

1889. On the osteology of *Steatornis caripensis*. Proc. Zool. Soc. London, 1889: 161-190.

Pietri, E. de B.

1957. El Guacharo (monografia). Bol. Soc. Venezolana Cienc. Nat., 18: 3-41.

Sclater, P. L.

1866. Notes on the American Caprimulgidae. Proc. Zool. Soc. London, 1866: 126-145.

Sibley, C. G.

1960. The electrophoretic patterns of avian egg-white proteins as taxonomic characters. Ibis, 102: 215-259.

Skutch, A. F.

1945. Incubation and nestling periods of Central American birds. Auk, 62: 8-37.

Snow, D.

1958. Trinidad's Oilbirds are yielding new facts. Animal Kingdom, 61: 117-121.

Stolzmann, J.

1880. Observations sur le Steatornis péruvien. Bull. Soc. Zool. France, 5: 198-204.

TACZANOWSKI, L.
1884. Ornithologie du Pérou. Vol. 1. Rennes.

WETMORE, A.
1918. On the anatomy of *Nyctibius* with notes on allied birds. Proc. U. S. Nat. Mus., 54: 577-586.

EXPLANATION OF THE PLATES

Plate I

Fig. 1. Typical stance of Oilbird on nest. Note position of feet far forward under breast.

Fig. 2. Oilbird clinging to narrow ledge; showing backward position of inner toe, and tail pressed against rock face. Feet are held much farther back than when perching on level surface (Fig. 1). For explanation see text.

Plate II

Fig. 3. Oilbirds clinging to sloping ledge; showing position of legs and toes. For explanation see text.

Fig. 4. Oilbird in slow flight, at early stage of upstroke; tip of left wing still on the downstroke. To show the extreme width of wing and fully spread tail.

Fig. 5. Oilbird in slow flight; the upstroke. The bend in the wing shows that the wing beat is propulsive.